Bull. Mus. natn. Hist. nat., Paris, 4e sér., **8**, 1986,
section A, n° 1 : 145-170.

New species of *Austrostrongylus* Chandler, 1924 (Nematoda, Trichostrongyloidea), from Australian Marsupials, with a redescription of *A. minutus* Johnston & Mawson, 1938, and description of a new genus, *Sutarostrongylus*

by Ian Beveridge and Marie-Claude Durette-Desset

Abstract. — The following new species of *Austrostrongylus* Chandler, 1924 (Nematoda, Trichostrongyloidea), are described from Australian Marsupials : *A. safestatus* sp. n. from *Petrogale persephone* Maynes, 1982, and *P. inornata* Gould, 1842 ; *A. petrogale* sp. n. from *Petrogale godmani* Thomas, 1923, *P. herberti* Thomas, 1926, and *P. assimilis* Ramsay, 1877 ; *A. bancrofti* sp. n. from *Macropus dorsalis* (Gray, 1837) ; *A. incurvispiculum* sp. n. from *Macropus fuliginosus* (Desmarest, 1817). *A. minutus* Johnston & Mawson, 1938, is redescribed from *Macropus dorsalis.* The genus is re-defined. *Sutarostrongylus kirkpatricki* gen. et sp. n. from *Thylogale thetis* (Lesson, 1827) is described. The new genus is distinguished from *Austrostrongylus* in the absence of body floats and in the presence of striated spicules. New records of *Paraustrongylus hypsiprymnodontis* (Mawson, 1973) comb. nov. are given. The evolution of the characteristic synlophe of *Austrostrongylus* is discussed and correlated with host evolution.

Résumé. — *Description de nouvelles espèces d'*Austrostrongylus *Chandler, 1924 (Nematoda, Trichostrongyloidea), parasites de Marsupiaux australiens, redescription d'*A. minutus *Johnston & Mawson, 1938, et description d'un nouveau genre,* Sutarostrongylus. — Quatre espèces nouvelles d'*Austrostrongylus* Chandler, 1924 (Nematoda, Trichostrongyloidea), parasites de Marsupiaux australiens, sont décrites : *A. safestatus* sp. n. parasite de *Petrogale persephone* Maynes, 1982, et *P. inornata* Gould, 1842 ; *A. petrogale* sp. n. parasite de *Petrogale godmani* Thomas, 1923, *P. herberti* Thomas, 1926, et *P. assimilis* Ramsay, 1877 ; *A. bancrofti* sp. n. parasite de *Macropus dorsalis* (Gray, 1837) ; *A. incurvispiculum* sp. n. parasite de *Macropus fuliginosus* (Desmarest, 1817). *A. minutus* Johnston & Mawson, 1938, est redécrit du matériel provenant de *Macropus dorsalis.* Le genre est redéfini. *Sutarostrongylus kirkpatricki* gen. et sp. n., parasite de *Thylogale thetis* (Lesson, 1827) est décrit. Le nouveau genre se distingue d'*Austrostrongylus* par l'absence de flotteurs et la présence de spicules striés. L'évolution du synlophe d'*Austrostrongylus* est décrite et comparée avec l'évolution des hôtes.

I. Beveridge and M. C. Durette-Desset, *Laboratoire des Vers, Associé au CNRS, Muséum national d'Histoire naturelle, 61, rue Buffon, F 75231 Paris cedex 05.*

The trichostrongyloid nematode genus *Austrostrongylus* Chandler, 1924, occurs principally in the small intestine of wallabies (Macropodidae), with most of the currently known nematode species coming from hosts in southeastern Australia. Mawson (1973) undertook a major review of the genus and recognised the following species as valid : *A. aggregatus* Johnston and Mawson, 1940, *A. chandleri* Mawson, 1973, *A. hypsiprymnodontis* Mawson, 1973, *A. macropodis* Chandler, 1924, *A. minutus* Johnston and Mawson, 1938, *A. paratypicus* Mawson, 1973, and *A. thylogale* Johnston and Mawson, 1940. Because of the unique body floats

(= flotteurs) present in species of the genus, DURETTE-DESSET (1979) redescribed the synlophe in several species and HUMPHERY-SMITH (1980) described additional details of the synlophe of *A. hypsiprymnodontis*. More recently, CASSONE (1983) added a new species, *A. victoriensis* Cassone, 1983, from a wallaby, *Wallabia bicolor* (Desmarest, 1804) and BEVERIDGE and DURETTE-DESSET (1985) described a new species, *A. notoryctis* Beveridge and Durette-Desset, 1985, from the marsupial mole, *Notoryctes typhlops* (Stirling, 1899).

In this paper we describe four new species of *Austrostrongylus*, give a redescription of *A. minutus*, which was not considered in detail by MAWSON (1973), and propose a new genus, *Sutarostrongylus*, for a new species which we consider ancestral to *Austrostrongylus*. Of the new species of *Austrostrongylus*, two come from rock wallabies of the genus *Petrogale* and have a number of morphological features which we consider primitive when compared with species already described from those wallabies belonging to the genus *Macropus*.

Measurements are given in the text in millimetres, as the range of five measurements followed by the mean in parentheses. Specimens have been deposited in the South Australian Museum, Adelaide (SAM), the Muséum national d'Histoire naturelle, Paris (MNHN) and the Australian Helminthological Collection, Adelaide (AHC). Scale lines of all figures are in millimetres.

SUTAROSTRONGYLUS gen. n.

DEFINITION : Trichostrongyloidea, Herpetostrongylidae. Small worms coiled ventrally in spiral ; mouth opening with six lips ; buccal capsule subglobular, well sclerotised, with dorsal ad two subventral teeth ; cephalic vesicle prominent ; synlophe oriented frontally ; four ventral ridges oriented towards the left ; two dorsal ridges oriented towards the left ; lateral body floats absent ; spicules simple, with prominently striated alae ; dorsal lobe of bursa small, thickened ; ray 2 not markedly divergent from remaining rays ; dorsal ray (9) with three pairs of branches ; genital cone not sclerotised ; vulva in posterior part of body ; didelphic ; parasitic in small intestine of macropodine marsupials.

TYPE SPECIES : *Sutarostrongylus kirkpatricki* sp. n.

Sutarostrongylus kirkpatricki gen. et sp. n.

(Fig. 1)

TYPES : Holotype ♂, allotype ♀, from small intestine of *Thylogale thetis* (Lesson) ; Emuvale, Queensland, 27.VIII.1975, coll. I. BEVERIDGE, in SAM n° V3618-3619. Paratypes : 1 ♂, in MNHN 808 CA ; 1 ♂, 1 ♀, dissected, slides, AHC S2437.

MATERIAL EXAMINED : Types.

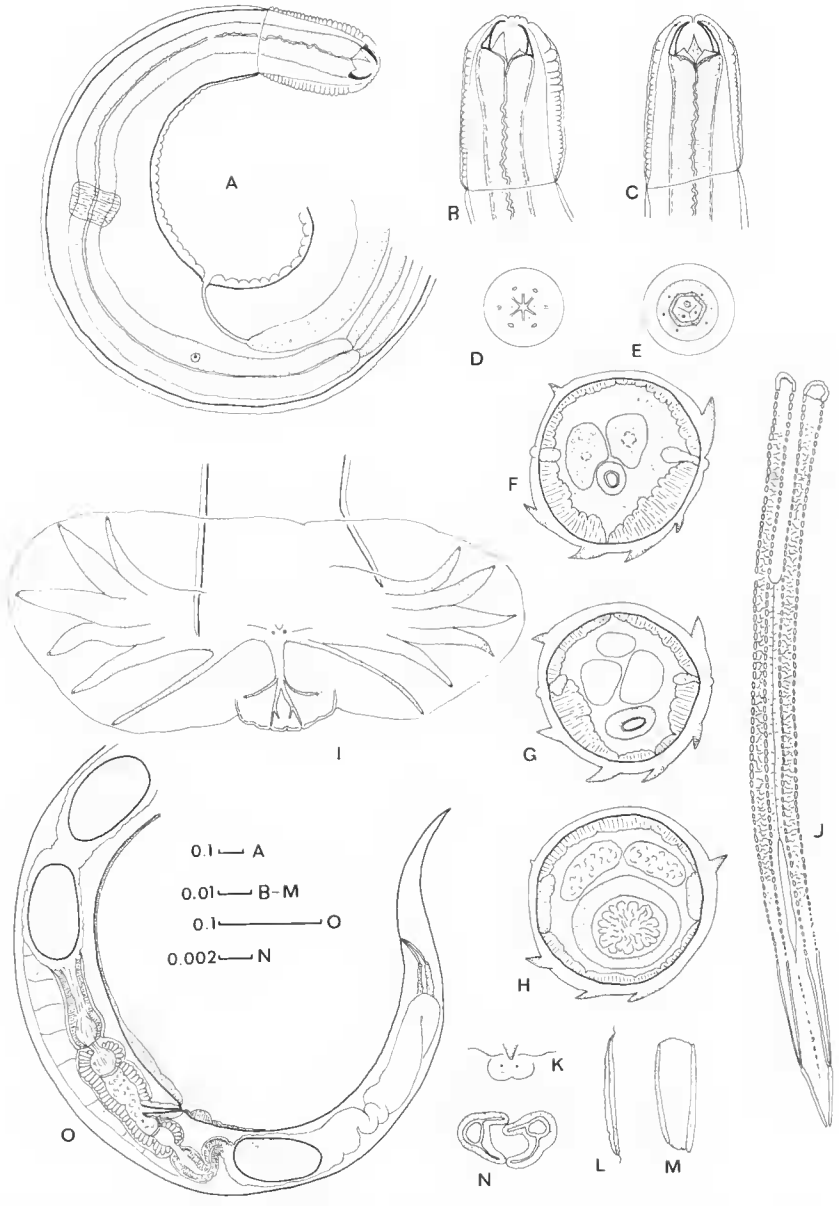

FIG. 1. — *Sutarostrongylus kirkpatricki* sp. n. : A, anterior end, lateral view ; B, head, lateral view ; C, head, ventral view ; D, mouth, apical view ; E, transverse optical section of buccal capsule ; F, transverse section of body, ♂, anterior end ; G, transverse section of body, ♀, anterior end ; H, transverse section of body, ♀, at level of ovejector, showing only 3 ventral ridges ; I, bursa, ventral view ; J, spicules, ventral view ; K, genital cone, ventral view ; L, gubernaculum, lateral view ; M, gubernaculum, ventral view ; N, transverse section of spicules ; O, tail, ♀, lateral view. Scale lines in mm.

Description

Small nematodes, coiled ventrally 3-4 times in tight spiral.

Synlophe : Similar in both sexes, with six ridges beginning posterior to cephalic vesicle, ending anterior to bursa in male, between vulva and anus in female ; lateral floats entirely absent ; ventral surface with four ridges oriented from right to left, diminishing in size from left to right ; 4th ridge disappears at level of vulva in female ; dorsal surface with one small left ridge and one larger right ridge, both orientated towards the left.

Head : Mouth opening with six small, subtriangular lips, each with internal labial papilla at base ; two amphids and four submedian papillae present external to lips. Buccal capsule small, sub-globular, walls well sclerotised, sub-hexagonal in transverse section ; single dorsal tooth and two smaller subventral teeth project into buccal capsule ; cephalic vesicle prominent ; oesophagus slender, claviform ; nerve ring in mid-oesophageal region ; excretory pore in posterior oesophageal region ; deirids at level of excretory pore.

Male : Length 2.9, 3.1, 3.1 ; cephalic vesicle 0.04, 0.05, 0.06 ; buccal capsule 0.009, 0.010, 0.012 × 0.015, 0.017, 0.018 ; dorsal tooth 0.005, 0.007, 0.007 ; oesophagus 0.36, 0.40, 0.40 ; nerve ring 0.16, 0.17, 0.17 from anterior end ; excretory pore 0.25, 0.26 from anterior end ; deirids 0.27 from anterior end ; spicules 0.23, 0.25, 0.27 simple ; calomus 0.07, 0.07, 0.07 long, lamina 0.16, 0.18, 0.20 with 2 alae, joined in mid-line ; alae with prominent irregular and very coarse transverse striations ; striations fine, longitudinal — oblique distally ; spicule tips single, each with needle-like projection. Gubernaculum quadrangular, 0.030, 0.035, 0.047 long. Bursa symmetrical, dorsal lobe small, greatly thickened ; rays 2 and 3 slender, divergent ; ray 4 thicker ; ray 5 turned dorsally near extremity ; ray 6 slender, straight ; ray 8 filiform, straight, arising with lateral rays ; ray 9 slender, lateral branches arising at main bifurcation ; main branches attain margin of bursa, each with short internal branch at mid-length. Genital cone small, non sclerotised.

Female : Length 2.9, 2.9 ; cephalic vesicle 0.05, 0.06 ; buccal capsule 0.010, 0.011 × 0.016, 0.018 ; dorsal tooth 0.008, 0.008 ; oesophagus 0.45, 0.53 ; nerve ring 0.13, 0.17 from anterior end ; excretory pore 0.25, 0.26 from anterior end ; deirids 0.25 from anterior end ; tail simple, tapering 0.11, 0.12 long ; vulva 0.37, 0.45 from posterior end ; *vagina vera* short, 0.035, 0.035 ; didelphic ; ovejector asymmetrical, anterior part 0.045, 0.050, posterior part 0.020, 0.015 long ; anterior uterus 0.26, 0.29 long with 3-4 eggs ; posterior uterus 0.10, 0.11 long with 1 egg ; eggs 0.070, 0.075 × 0.030, 0.035.

Discussion

Sutarostrongylus kirkpatricki is distinguished from *Austrostrongylus* by spicules and synlophe. It is unique in possessing spicules with heavily striated alae, a character which is immediately obvious even at low magnification, and lacks lateral floats at any level of the body, a character present in all species of *Austrostrongylus*. Nevertheless, the basic features of the synlophe, in particular the four ventral, left-oriented ridges, frontal axis of orientation of the synlophe, and the inflated dorsal lobe of the bursa are similar to species

of *Austrostrongylus*. The dorsal surface of *S. kirkpatricki* has one less ridge than *A. safestatus*, but the relative sizes and orientation of the ridges are otherwise similar. Apart from the frontal rather than oblique axis of orientation, the synlophe of *S. kirkpatricki* is identical with *Dessetostrongylus moorhousei* Humphery-Smith, 1980, a parasite of *Antechinus swainsonii* (Waterhouse, 1840), and the latter species also has faintly striated spicules.

A generic definition is given.

The new species is named after Dr. T. H. KIRKPATRICK who collected the host animal from which the parasites were obtained.

Sutarostrongylus sp.

MATERIAL EXAMINED : From *Thylogale stigmatica* Gould, 1860 ; Queensland : 1 ♂, Peeramon, 19.VI.1978, coll. P. M. JOHNSON (AHC 8961), 1 ♀, Wongabel State Forest, Atherton, June 1982, coll. S. HOUSE (AHC 12355).

DISCUSSION

A full description of this species cannot be given since the only two specimens available are both damaged. However, it is of interest, since the synlophe consists of four ventral and two dorsal body ridges without any evidence of lateral floats. The species is therefore similar to *S. kirkpatricki*, and in addition has prominently striated spicules. The spicules are longer than those of *S. kirkpatricki* and the tips are different, hence the species is certainly new, but more specimens will have to be collected before a full description can be given.

The interest of the species lies in the fact that, like *S. kirkpatricki*, it lacks body floats and occurs in the genus *Thylogale*.

AUSTROSTRONGYLUS Chandler, 1924

REDEFINITION OF *Austrostrongylus* : Trichostrongyloidea, Herpetostrongylidae. Small worms usually coiled ventrally in spiral ; mouth opening with six lips ; buccal capsule subglobular, well sclerotised, with dorsal and two subventral teeth : cephalic vesicle prominent ; synlophe orientated frontally ; three or four ventral ridges orientated towards the left, decreasing in size from left to right ; two or more dorsal ridges present ; one or two lateral body floats present, spicules simple, nonstriated ; dorsal lobe of bursa small, characteristically thickened ; ray 2 not markedly divergent from remaining rays ; dorsal ray (9) with three pairs of branches ; genital cone not sclerotised ; vulva in posterior part of body ; usually didelphic, rarely monodelphic ; parasitic in small intestine of macropodine marsupials and in *Notoryctes typhlops* (Notoryctidae).

Austrostrongylus safestatus sp. n.

(Fig. 2)

TYPES : Holotype ♂, allotype ♀, from small intestine of *Petrogale persephone* Maynes, 1982 ; Proserpine, Queensland, 7.III.1978, coll. P. M. JOHNSON and D. M. SPRATT, in SAM n° V 3584-3585. Paratypes : 5 ♂, 5 ♀, in SAM n° V 3586-3595 ; 5 ♂, 5 ♀, in MNHN n° 539 HD ; 10 ♂, 15 ♀, in AHC n° 13753.

MATERIAL EXAMINED : From *Petrogale persephone* : Types. — From *Petrogale inornata* Gould, 1842 ; Queensland : 3 ♂, 3 ♀, Byrne Valley Station via Home Hill, 1.VII.1983, 3.VII.1983, coll. S. BARKER ; 1 ♂, 3 ♀, Mt. Johnycake via Collinsville, 5.VII.1983, coll. S. BARKER.

DESCRIPTION

Small nematodes, coiled ventrally in spiral of 4-5 turns.

Synlophe : six ridges present in mid-body region ; three principal ventral ridges, directed towards left arise posterior to cephalic vesicle ; three small ridges on dorsal surface, two on right side, one on left, directed towards left ; small left dorsal ridge absent anterior to nerve ring in female ; in posterior body, dorsal ridges lost ; in female, one ventral ridge lost anterior to vulva ; posterior to vulva, additional ventral ridge lost leaving single ridge. Single float present on left side of body ; vestigial in anterior part of body in males and females ; inflated in posterior part of body of male, to lesser extent in female.

Head : Mouth opening small, surrounded by six small, sub-triangular lips, each with tiny internal labial papilla at base ; two amphids and four submedian papillae present external to lips. Buccal capsule small, sub-globular, walls heavily sclerotised, sub-hexagonal in transverse section ; single dorsal tooth and two small sub-ventral teeth project into buccal capsule ; cephalic vesicle prominent ; oesophagus slender, claviform ; nerve ring in mid oesophageal region ; excretory pore in posterior oesophageal region ; deirids at level of excretory pore.

Male : Length 3.2-4.0 (3.6) ; cephalic vesicle 0.060-0.075 (0.068) long ; buccal capsule 0.012-0.015 (0.014) × 0.014-0.025 (0.021) ; dorsal tooth 0.006-0.010 (0.008) ; oesophagus 0.35-0.43 (0.39) ; nerve ring 0.14-0.20 (0.18) from anterior end ; excretory pore 0.24-0.32 (0.29) from anterior end ; deirids 0.27 from anterior end ; spicules 0.22-0.25 (0.23) long, slender ; calomus short, 0.05-0.06 (0.055) long ; lamina 0.16-0.19 (0.17) long with slender alae ; spicule tips simple, blent ; gubernaculum long, slender, 0.040-0.055 (0.051). Bursa symmetrical, dorsal lobe small, slightly thickened ; rays 2 and 3 slender, terminate separately ; rays 4 and 5 broader, ray 5 directed posteriorly at termination : ray 6 slender, straight, filiform, arising close to base of ray 9 ; ray 9 slender, with fine recurved lateral branches arising near origin ; main bifurcation at midlength, with pair of short internal branches arising after main bifurcation. Genital cone, small, non-sclerotised.

Female : Length 4.5-5.1 (4.9) ; cephalic vesicle 0.070-0.085 (0.080) ; buccal capsule 0.014-0.019 (0.016) × 0.024-0.029 (0.026) ; dorsal tooth 0.010-0.012 (0.011) ; oesophagus

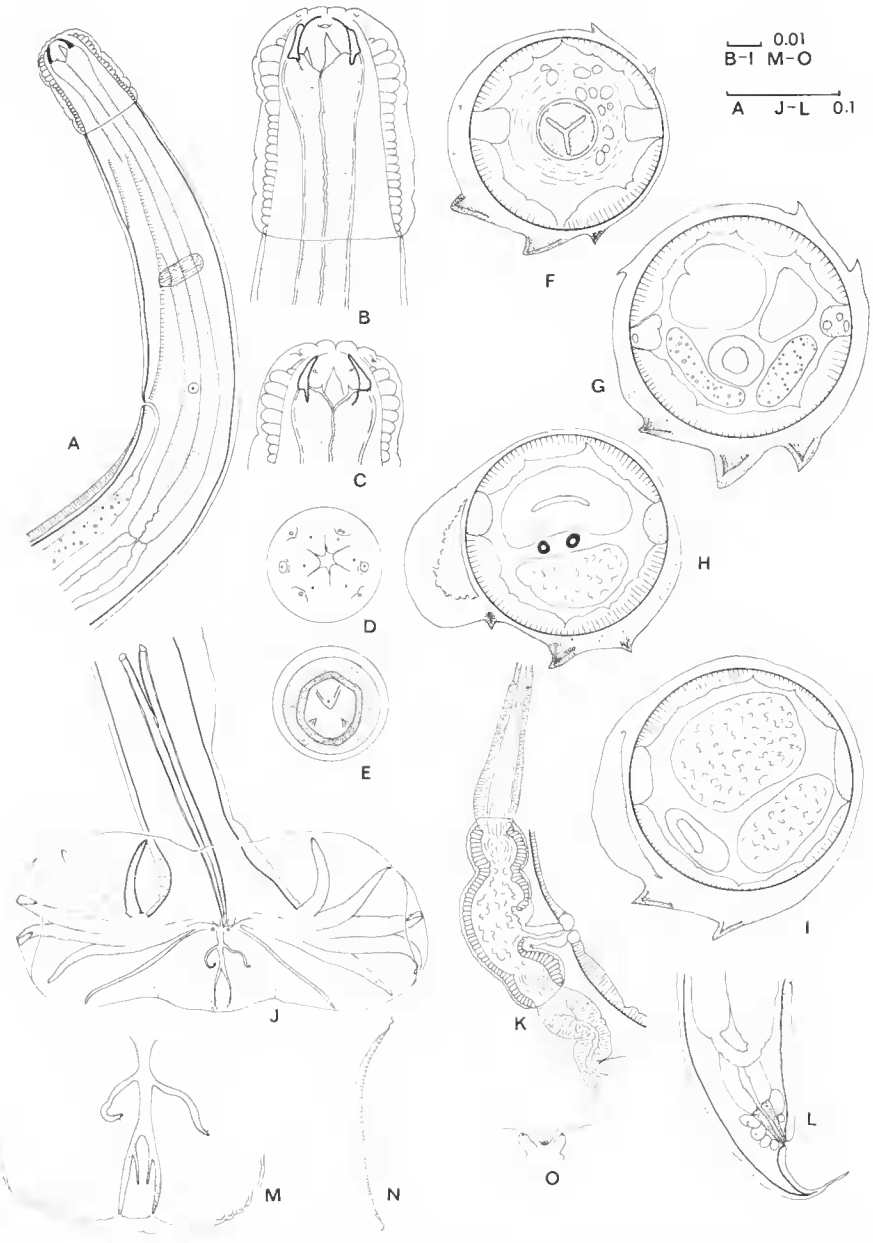

FIG. 2. — *Austrostrongylus safestatus* sp. n. : A, anterior end, ♂, lateral view ; B, head, ♀, lateral view ; C, head ♂, ventral view ; D, mouth, apical view ; E, optical transverse section through buccal capsule and teeth ; F, transverse section of body at level of nerve ring, ♀ ; G, transverse section of body, anterior end, ♂ ; H, transverse section of posterior region of body, ♂ ; I, transverse section of body, anterior to vulva, ♀ ; J, bursa, ventral view ; K, ovejector, lateral view ; L, female tail, lateral view ; M, dorsal lobe of bursa and dorsal ray, dorsal view ; N, gubernaculum, lateral view ; O, genital cone, ventral view. Scale lines in mm.

0.40-0.53 (0.44) ; nerve ring 0.17-0.19 (0.18) from anterior end ; excretory pore 0.25-0.37 (0.31) from anterior end ; deirids 0.30, 0.33 from anterior end ; tail 0.03-0.06 (0.05) long, simple, tapering ; vulva 0.52-0.71 (0.59) from posterior end ; vulval lips not prominent, *vagina vera* 0.035-0.050 (0.040) ; didelphic ; ovejector asymmetrical, anterior part 0.17, 0.17 ; posterior part 0.11, 0.16 ; anterior infundibulum slightly longer 0.080-0.090 (0.085) than posterior, 0.055-0.080 (0.069) ; anterior uterus 0.55, 0.85 with 5-7 eggs ; posterior uterus 0.22, 0.50 with 2-4 eggs ; eggs 0.070-0.075 (0.073) × 0.040-0.045 (0.043).

Discussion

A. safestatus sp. n. belongs to a group of species with short spicules, comprising *A. thylogale, A. notoryctis, A. victoriensis, A. minutus, A. bancrofti, A. petrogale* and *S. kirkpatricki*. It differs from *A. bancrofti* in having uniform spicule shafts, and from *A. notoryctis, A. victoriensis* and *A. thylogale* in having a symmetrical bursa. Spicule length (0.22-0.25 mm) separates the species from *A. minutus* (0.35-0.43 mm). *A. safestatus* is most similar to *A. petrogale* and both species occur in members of the genus *Petrogale*. Both species are also distinguished from congeners by the presence of a single, poorly developed body float. The two species can be differentiated from one another only by their synlophe. *A. petrogale* has nine ridges in the anterior part of the body rather than six. Fortunately, the material used to describe both species was relatively abundant and the differences in synlophe were stable in different host species and from different localities. *P. persephone* and *P. inornata*, the hosts of *A. safestatus*, occupy an intermediate range in Queensland, with hosts of *A. petrogale, P. godmani* and *P. assimilis* occurring to the north of them, and *P. herberti* occurring to the south (Sharman and Maynes, 1983 ; Maynes and Sharman, 1983 *a* & *b*).

Austrostrongylus petrogale sp. n.

(Fig. 3)

Types : Holotype ♂, allotype ♀, from small intestine of *Petrogale godmani* Thomas, 1923 ; Curraghmore Station via Mareeba, Queensland, 28.IV.1983, coll. S. Barker, in SAM n° V 3596, 3597. Paratypes : 5 ♂, 5 ♀, in SAM n° V 3598-3607 ; 5 ♂, 5 ♀, in MNHN n° 538 HD ; 32 ♂, 70 ♀, in AHC n° 13754.

Material examined : From *Petrogale godmani* : Queensland : 13 ♂, 5 ♀, Brooklyn Station via Mareeba, 26.IV.1983, 27.IV.1983, coll. S. Barker ; 1 ♂, 2 ♀, King's Plains Station via Cooktown, 1.V.1983, coll. S. Barker ; 3 ♂, 13 ♀, 15 km south of Laura, 6.VIII.1982, coll. R. Close ; 10 ♂, 14 ♀, Mt Elephant, Cooktown, 28.VII.1982, coll. R. Close ; 3 ♂, 13 ♀, McLeod River near Cooktown, 25.VII.1982, 26.VII.1982, coll. R. Close. — From *Petrogale assimilis* Ramsay, 1877 : Queensland : 25 ♂, 23 ♀, Boonderoo Station via Hughenden, 13.IV.1983, 15.IV.1983, 17.IV.1983, 18.IV.1983, coll. S. Barker ; 31 ♂, 26 ♀, Mt Claro, via Ingham, 13.V.1983, coll. S. Barker ; 3 ♂, 4 ♀, Valley of Lagoons Station, via Ingham, 11.V.1983, coll. S. Barker ; 5 ♂, 7 ♀, South Edge Station, via Mareeba, 25.IV.1983, coll. S. Barker ; 1 ♀, Ironhurst Station, via Georgetown, 20.VII.1984, coll. S. Barker ; 7 ♂, 15 ♀, Porcupine Gorge, Hughenden, 15.VIII.1984, 17.VIII.1984, coll. S. Bar-

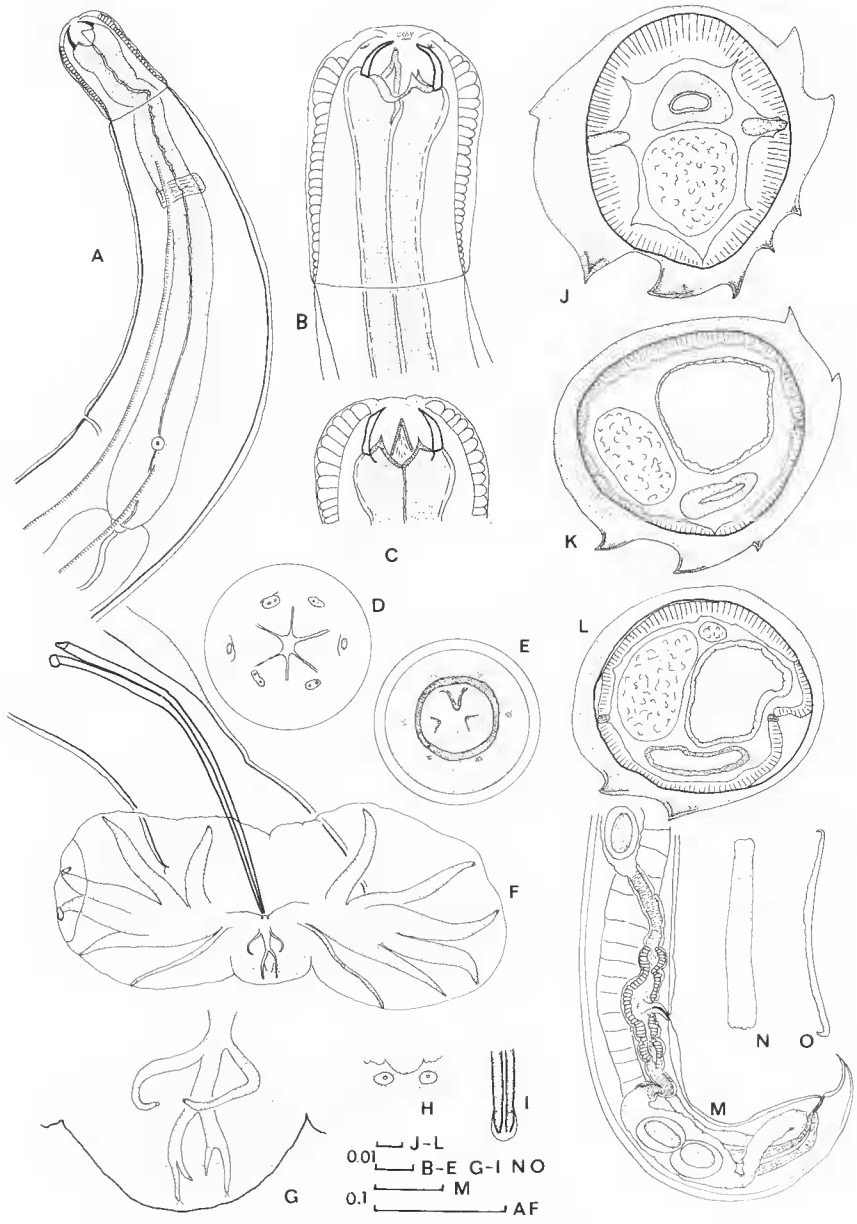

FIG. 3. — *Austrostrongylus petrogale* sp. n. : A, anterior end, lateral view ; B, head, lateral view ; C, head, ventral view ; D, mouth, apical view ; E, optical transverse section of buccal capsule and teeth ; F, bursa and spicules, ventral views ; G, dorsal lobe of bursa and dorsal ray, ventral view ; H, genital cone, ventral view ; I, spicule tips, ventral view ; J, transverse section of mid-body, ♂, ; K, transverse section of mid-body, ♀ ; L, transverse section of posterior part of body, ♀ ; M, female tail and ovejector, lateral view ; N, gubernaculum, ventral view ; O, gubernaculum, lateral view. Scale lines in mm.

KER ; 1 ♂, Clyde Park Station via Hughenden, 17.VIII.1984, coll. S. BARKER. — From *Petrogale herberti* Thomas, 1926 : Queensland : 1 ♀, Kinbombi Falls, Goomeri, 1.VI.1984, coll. R. CLOSE ; 2 ♂, 7 ♀, Laglan Station via Clermont, 1.IX.1984, coll. S. BARKER.

DESCRIPTION

Small nematodes, coiled ventrally 4-5 times in tight spiral.

Synlophe : Nine ridges present in anterior body region of both sexes : five ventral ridges present, directed to left, decreasing in size from left to right ; main ridges commence posterior to cephalic vesicle ; 4th commences at level of excretory pore ; 5th ridge smallest, present only in mid-body region, absent in most of body (fig. 3 J, K) ; two dorsal ridges on right side of body, directed to left ; float present on left side of body only ; small or vestigial in most regions, enlarged only in posterior region of body of male, with two ridges ; ridges diminish in size in mid and posterior region of male body but number remains constant (8) ; three ventral ridges and two right dorsal ridges in mid region of body of female, only two ventral ridges in posterior region.

Head : Mouth opening small, surrounded by six small, sub-triangular lips, each with tiny labial papilla at base ; two amphids and four double submedian papillae present external to lips. Buccal capsule small, sub-globular, walls heavily sclerotised, round to subhexagonal in transverse section. Single dorsal tooth and two small sub-ventral teeth project into buccal capsule ; cephalic vesicle prominent ; oesophagus slender, claviform ; nerve ring in anterior oesophageal region ; excretory pore in posterior oesophageal region ; deirids at level of excretory pore.

Male : Length 3.5-4.8 (4.2) ; cephalic vesicle 0.070-0.090 (0.078) buccal capsule 0.010-0.015 (0.014) ; oesophagus 0.30-0.50 (0.41) ; nerve ring 0.25 from anterior end ; excretory pore 0.20-0.50 (0.34) from anterior end ; deirids 0.45 from anterior end ; spicules 0.23-0.28 (0.26), slender ; calomus 0.07-0.09 (0.08) ; lamina 0.16-0.20 (0.18) with slender alae ; spicule tips simple, blunt, united in single transparent enlargement at tip ; gubernaculum 0.055-0.065 (0.060), slender. Bursa symmetrical, dorsal lobe small, thickened ; rays 2 and 3 slender, terminate separately ; rays 4 and 5 broader, termination of ray 5 deflected posteriorly ; ray 6, slender, straight ; ray 8 filiform, arising close to base of ray 9 ; ray 9 slender, with two recurved lateral branches arising near origin ; main bifurcation at mid-length, with pair of short internal branches arising after main bifurcation. Genital cone small, non-sclerotised.

Female : Length 4.9-6.6 (5.8) ; cephalic vesicle 0.08-0.10 (0.09) ; buccal capsule 0.010-0.015 (0.013) × 0.025-0.030 (0.026) ; dorsal tooth 0.015-0.025 (0.018) ; oesophagus 0.38-0.50 (0.45) ; nerve ring 0.21 from anterior end ; excretory pore 0.31-0.40 (0.36) from anterior end ; deirids 0.42 from anterior end ; tail 0.09-0.14 (0.11) long, simple, tapering ; vulva 0.56-0.70 (0.62) from posterior end ; *vagina vera* 0.03-0.04 (0.04) ; didelphic ; ovejector slightly asymmetrical, anterior part 0.09-0-11 (0.10), posterior part 0.07-0.08 (0.08) ; anterior uterus 0.87, 0.80 with single row of 8-14 eggs ; posterior uterus 0.18, 0.22 with 2-4 eggs ; eggs 0.08-0.09 (0.09) × 0.06.

Discussion

The short spicules of *A. petrogale* (0.23-0.28 mm) distinguish the species from all others except *A. thylogale, A. notoryctis, A. victoriensis, A. minutus, A. bancrofti*, and *A. safestatus*. The new species differs from *A. bancrofti* in having simple, uniform, non-striated spicules, and from *A. notoryctis, A. victoriensis* and *A. thylogale* in having a symmetrical bursa. Spicule length separates the new species from *A. minutus* (0.35-0.43 mm) and it is most similar morphologically to *A. safestatus*, also from *Petrogale* spp. The presence of a single left body float also separates *A. petrogale* from all congeners except *A. safestatus*. The two species can be separated by their synlophe, since *A. petrogale* has nine ridges in the anterior body region whereas *A. safestatus* has only six. This difference is constant in the material examined, which comes from a wide geographic range and from different host species, and is therefore considered a reliable specific character.

Austrostrongylus bancrofti sp. n.

(Fig. 4)

Types : Holotype ♂, allotype ♀, from small intestine of *Macropus dorsalis* (Gray, 1837) ; Eidsvold, Queensland, August 1918, coll. T. L. Bancroft, in SAM n° V 3614, 3615. Paratypes, 1 ♂, 1 ♀, in SAM n° V 3616, 3617 ; 7 ♂, 4 ♀, in AHC n° 13663 and 3110 ; 2 ♂ on slides, AHC n° 2463.

Material examined : From *Macropus dorsalis* ; Queensland : 11 ♂, 6 ♀, types ; 4 ♂, 2 ♀, Logan Village, May 1960, coll. M. J. Mackerras, in AHC n° 13664 and MNHN n° 536 HD.

Description

Small nematodes coiled ventrally four or five times in tight spiral.

Synlophe : Two large lateral floats extend along full length of body from cephalic vesicle to bursa in male, beyond vulva in female ; two large dorsal ridges and single ventral ridge on right float in mid-body region ; single ventral ridge on left float ; dorsal surface of body without ridges ; ventral surface with four ridges orientated from right to left, diminishing in size from left to right ; two smallest ridges absent in posterior part of body ; median dorsal ridge of right float present only in mid-body region, absent in oesophageal region and in posterior part of body.

Head : Mouth opening small, surrounded by six small, sub-triangular lips, each with tiny internal labial papilla at base ; two amphids and four submedian papillae present external to lips. Buccal capsule small, sub-globular, walls well sclerotised, sub-hexagonal in transverse section ; single dorsal tooth and two small ventral teeth project into buccal capsule ; cephalic vesicle prominent ; oesophagus slender, claviform ; nerve ring in anterior oesophageal region ; excretory pore in mid-oesophageal region ; deirids at level of excretory pore.

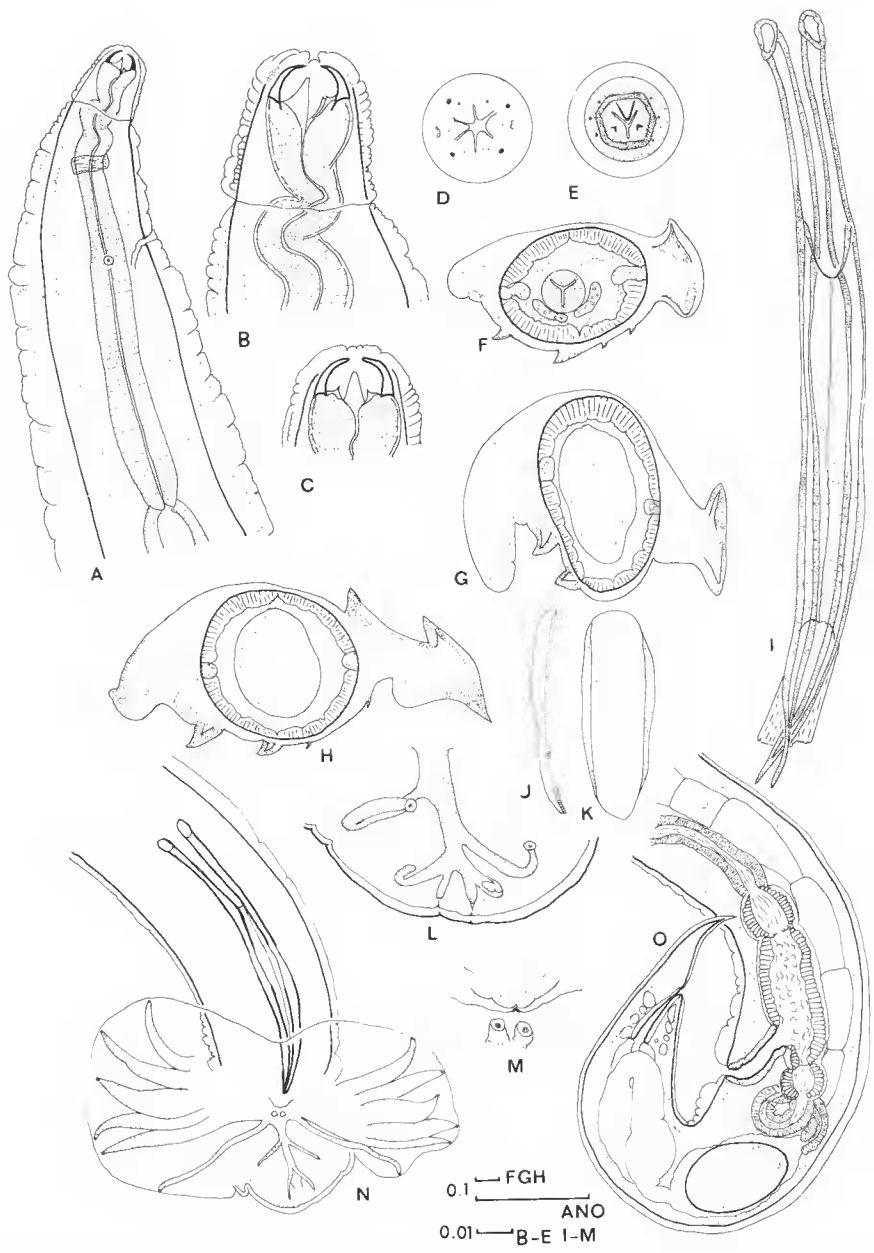

FIG. 4. — *Austrostrongylus bancrofti* sp. n. : A, anterior end, lateral view ; B, head, lateral view ; C, head, ventral view ; D, mouth, apical view ; E, optical transverse section through buccal capsule ; F, transverse section of body, ♂, oesophageal region, posterior to excretory pore ; G, transverse section of body, ♀, posterior end ; H, transverse section of mid-body, ♂ ; I, spicules, ventral view ; J, gubernaculum, lateral view ; K, gubernaculum, ventral view ; L, dorsal lobe of bursa, dorsal view ; M, genital cone, ventral view ; N, bursa and spicules, ventral view ; O, female tail, lateral view. Scale lines in mm.

Male : Length 2.8-3.4 (3.2) ; cephalic vesicle 0.05-0.07 (0.06) ; buccal capsule 0.015-0.020 (0.016) × 0.018-0.024 (0.021) ; dorsal tooth 0.009-0.010 (0.010) ; oesophagus 0.31-0.39 (0.34) ; nerve ring 0.06-0.11 (0.09) from anterior end ; excretory pore 0.17-0.24 (0.20) from anterior end ; deirids 0.17. 0.23 from anterior end ; spicules 0.20-0.25 (0.22) ; calomus 0.08-0.11 (0.09) ; lamina 0.12-0.15 (0.14), alate, alae joined medially ; mid region of spicule shaft markedly narrower, weakly sclerotised ; spicule tips simple, blunt ; alae end abruptly just anterior to spicule tips ; gubernaculum oval, much longer than broad, 0.06-0.07 (0.06). Bursa slightly asymmetrical : left lobe smaller than right ; dorsal lobe small, very thick ; rays 2 and 3 slender, terminate separately ; ray 4 broader than remaining rays, terminates short of bursal margin ; rays 5 and 6 slender, parallel ; ray 8 filiform, arising close to base of ray 9 ; ray 9 with elongate lateral branches arising at different levels, bifurcates near extremity into two recurved branches, each giving off short internal branch immediately after main bifurcation. Genital cone small, non-sclerotised.

Female : Length 3.5-3.9 (3.6) ; cephalic vesicle 0.05-0.07 (0.06) ; buccal capsule 0.012-0.020 (0.016) × 0.014-0.025 (0.021) ; dorsal tooth 0.010-0.015 (0.013) ; oesophagus 0.33-0.40 (0.35) ; nerve ring 0.09 from anterior end ; excretory pore 0.18 from anterior end ; deirids 0.17 from anterior end ; tail 0.07-0.09 (0.08) simple, tapering ; vulva 0.31-0.43 (0.38) from posterior end ; *vagina vera* short, 0.04, 0.05 ; ovejector asymmetrical, anterior part 0.11, longer than posterior part, 0.05 ; anterior uterus 0.45 with six or more eggs ; posterior uterus short, 0.15 with twelve eggs ; eggs 0.05, 0.08, 0.08 × 0.04, 0.04, 0.05.

Discussion

A. bancrofti belongs to a group of species with short, non-striated spicules which includes *A. minutus* (0.35-0.43 mm), *A. thylogale* (0.36-0.45 mm), *A. victoriensis* (0.32 mm), *A. safestatus* (0.22-0.25), *A. notoryctis* (0.23-0.27 mm) and *A. petrogale* (0.23-0.27 mm). The length of the spicules of *A. bancrofti*, 0.20-0.25 mm long, differentiates the species from all of these except *A. petrogale* and *A. safestatus*. The marked decrease in thickness of the mid-region of the spicule shafts of *A. bancrofti* is a consistent readily observed character which serves to differentiate it from all congeners. In addition, its synlophe with the two floats and eight ridges characteristic of the genus separates *A. bancrofti* from *A. petrogale* and *A. safestatus*.

A. bancrofti occurs in mixed infections with *A. minutus* in *Macropus dorsalis*. The males are readily distinguished by spicule lengths, while the females can be distinguished by body shape (see below) and by the sub-ventral teeth which are much large in *A. minutus*.

The synlophe differs slightly in different regions of the body. The medial dorsal ridge on the right float is present in the mid-body region only, while the third and fourth ventral body ridges are absent in the posterior part of the body. The same pattern occurs in the synlophe of *A. minutus* also.

Austrostrongylus minutus Johnston & Mawson, 1938

(Fig. 5)

Material examined : From *Macropus dorsalis* ; Queensland : 2 ♂, 10 ♀, Eidsvold, August 1918, coll. T. L. Bancroft (AHC 85, MNHN 540 HD) ; 1 ♂, pieces of 3 ♂♂, Logan Village, May 1960, coll. M. J. Mackerras (AHC 2655).

Description

Small nematodes, coiled ventrally two or three times in very loose, flat coil.

Synlophe : In both sexes two large lateral floats and eight cuticular ridges in mid-body region ; floats begin posterior to cephalic vesicle and extend to bursa in male, to rectum in female ; two large dorsal ridges and one large ventral ridge on right float ; single ventral ridge on left float ; dorsal surface of body without ridges ; ventral surface with four ridges orientated from right to left, diminishing in size from left to right ; two smallest ridges disappear in posterior region of body of male ; median dorsal ridge of right float present only in mid-body region ; absent in region of oesophagus and in posterior part of body.

Head : Mouth opening with six small, sub-triangular lips, each with internal labial papilla at base ; two amphids and four submedian papillae present external to lips. Buccal capsule small, sub-globular, walls well sclerotised, sub-hexagonal in transverse section ; single dorsal tooth and two smaller sub-ventral teeth project into buccal capsule ; cephalic vesicle prominent ; oesophagus slender, claviform ; nerve ring in anterior oesophageal region ; excretory pore in mid-oesophageal region ; deirids at level of excretory pore.

Male : Length 2.7-3.8 (3.1) ; cephalic vesicle 0.05-0.07 (0.06) ; buccal capsule 0.013-0.016 (0.015) × 0.015-0.024 (0.019) ; dorsal tooth 0.008-0.012 (0.010) ; oesophagus 0.29-0.35 (0.31) ; nerve ring 0.10-0.14 (0.12) from anterior end ; excretory pore 0.22, 0.23, 0.25 from anterior end ; deirids 0.14, 0.16 from anterior end ; spicules 0.35-0.42 (0.40) simple ; calomus 0.09-0.11 (0.10) ; lamina 0.28-0.34 (0.31) alate ; spicule tips blunt, alae end at tips. Gubernaculum seen in single specimen only, 0.17 long. Bursa symmetrical ; dorsal lobe greatly thickened, small ; ray 2 slender, anterolateral, divergent from ray 3 ; rays 3 and 4 very broad ; ray 5 narrower, termination deflected dorsally ; ray 6 slender ; ray 8 filiform, arising close to dorsal ray ; ray 9 gives off lateral branches at different levels, divides at 3/4 length into two recurved branches each giving off short internal branch soon after main bifurcation. Genital cone small, non-sclerotised.

Female : Length 3.2-3.9 (3.7) ; cephalic vesicle 0.05-0.07 (0.06) ; buccal capsule 0.012-0.020 (0.016) × 0.020-0.025 (0.023) ; dorsal tooth 0.010-0.013 (0.011) ; oesophagus 0.32-0.40 (0.35) ; nerve ring 0.09, 0.11 from anterior end ; excretory pore 0.21, 0.32 from anterior end ; deirids 0.20 from anterior end ; tail 0.06-0.10 (0.08) simple, tapering ; vulva 0.35-0.41 (0.38) from posterior end ; *vagina vera* 0.04, 0.05 long ; didelphic ; ovejector very slightly asymmetrical with anterior part 0.06, 0.08, posterior part 0.05, 0.07 ; anterior uterus up to 0.45, much longer than posterior uterus, 0.24 ; anterior uterus with six or more eggs, posterior uterus with one-two ; eggs 0.07-0.08 (0.075) × 0.04-0.06 (0.05).

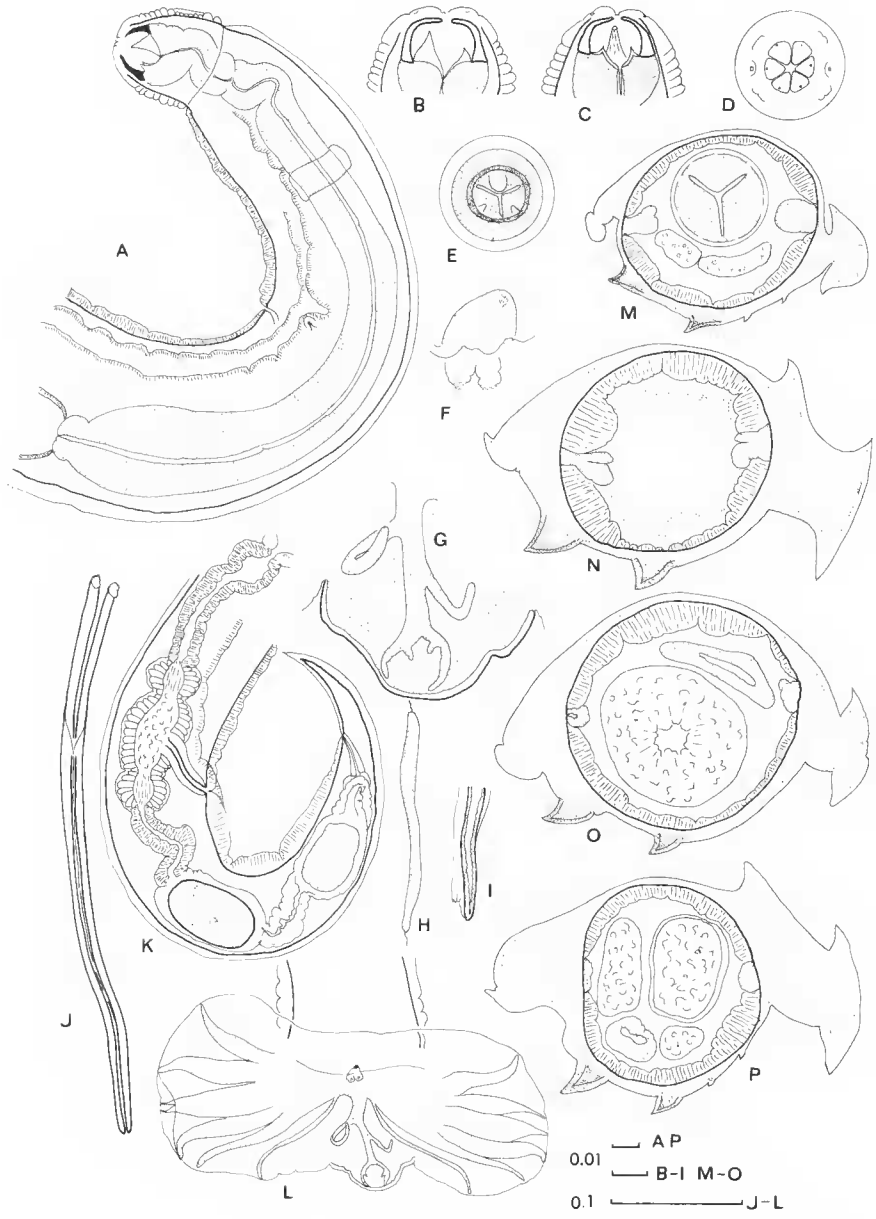

FIG. 5. — *Austrostrongylus minutus* Johnston & Mawson, 1938 : A, anterior end, lateral view ; B, head, lateral view ; C, head, ventral view ; D, mouth, apical view ; E, optical transverse section through buccal capsule and teeth ; F, genital cone, ventral view ; G, dorsal lobe of bursa and dorsal ray, dorsal view ; H, gubernaculum, lateral view ; I, spicule tip, lateral view ; J, spicules, ventral view ; K, female tail and ovejector, lateral view ; L, bursa, ventral view ; M, transverse section of body, ♂, through oesophageal region ; N, transverse section of mid-body, ♂, ; O, transverse section of body, ♂, posterior end ; P, transverse section of mid-body, ♀. Scale lines in mm.

Discussion

A. minutus belongs to a group of species with spicules less than 0.5 mm long ; namely *A. victoriensis* (0.32 mm), *A. bancrofti* (0.20-0.25 mm), *A. notoryctis* (0.23-0.27 mm), *A. thylogale* (0.36-0.45 mm), *A. safestatus* (0.22-0.25) and *A. petrogale* (0.23-0.27 mm). Its spicule length (0.35-0.43 mm) clearly separates it from each of these species except *A. thylogale*. The lack of two lateral floats in the synlophe of *A. safestatus* and *A. petrogale* distinguishes them immediately from *A. minutus* which has a synlophe of eight ridges and two floats typical of the genus (Mawson, 1973 ; Durette-Desset, 1979 ; Cassone, 1983). *A. minutus* is also distinguished from *A. victoriensis* and *A. bancrofti* by its symmetrical bursa, from *A. bancrofti* in that the spicule shafts of *A. minutus* are of equal thickness throughout their lengths, and from *A. victoriensis* in that the right ray 2 of the bursa of *A. minutus* is not thickened as it is in *A. victoriensis*. *A. minutus* is distinguished from *A. thylogale* by its symmetrical bursa and by the dorsal ray, which reaches the margin of the bursa in *A. minutus*, but not in *A. thylogale*.

In identifying mixed infections of *A. minutus* and *A. bancrofti*, the spicules allow ready separation of the males, while the females are best separated by the shape of the body, which is coiled in the form of a tight spiral in *A. bancrofti*, but in two or three loose open coils in *A. minutus*. The dorsal ridge on the right float is present only in the mid-body region of this species, hence in determining the number of body ridges, it is essential that sections are taken in this region. Similarly, the third and fourth ventral body ridges disappear in the posterior part of the body. The same changes in the synlophe occur in *A. bancrofti*.

Austrostrongylus incurvispiculum sp. n.

(Fig. 6)

Types : Holotype ♂, allotype ♀, from duodenum of *Macropus fuliginosus* (Desmarest, 1817) ; Dungunna via Cranbourne, Western Australia, 12.V.1981, coll. P. M. Mawson, in SAM n° V 3645-3646 ; paratypes : 2 ♂, 2 ♀, in SAM n° V 3647-3650 ; 1 ♂, 1 ♀, in MNHN n° 537 HD ; 2 ♂, 2 ♀, in AHC n° 8676.

Description

Small nematodes coiled ventrally two or three times in loose coil.

Synlophe : Two large lateral floats and eight cuticular ridges present in both sexes ; floats and ridges begin posterior to cephalic vesicle, extend almost to bursa in male, to vulva in female ; two large dorsal ridges and one large ventral ridge on right float, single ridge in lateral position on left float ; dorsal surface of body without ridges ; ventral surface with four ridges orientated from right to left, diminishing in size from left to right.

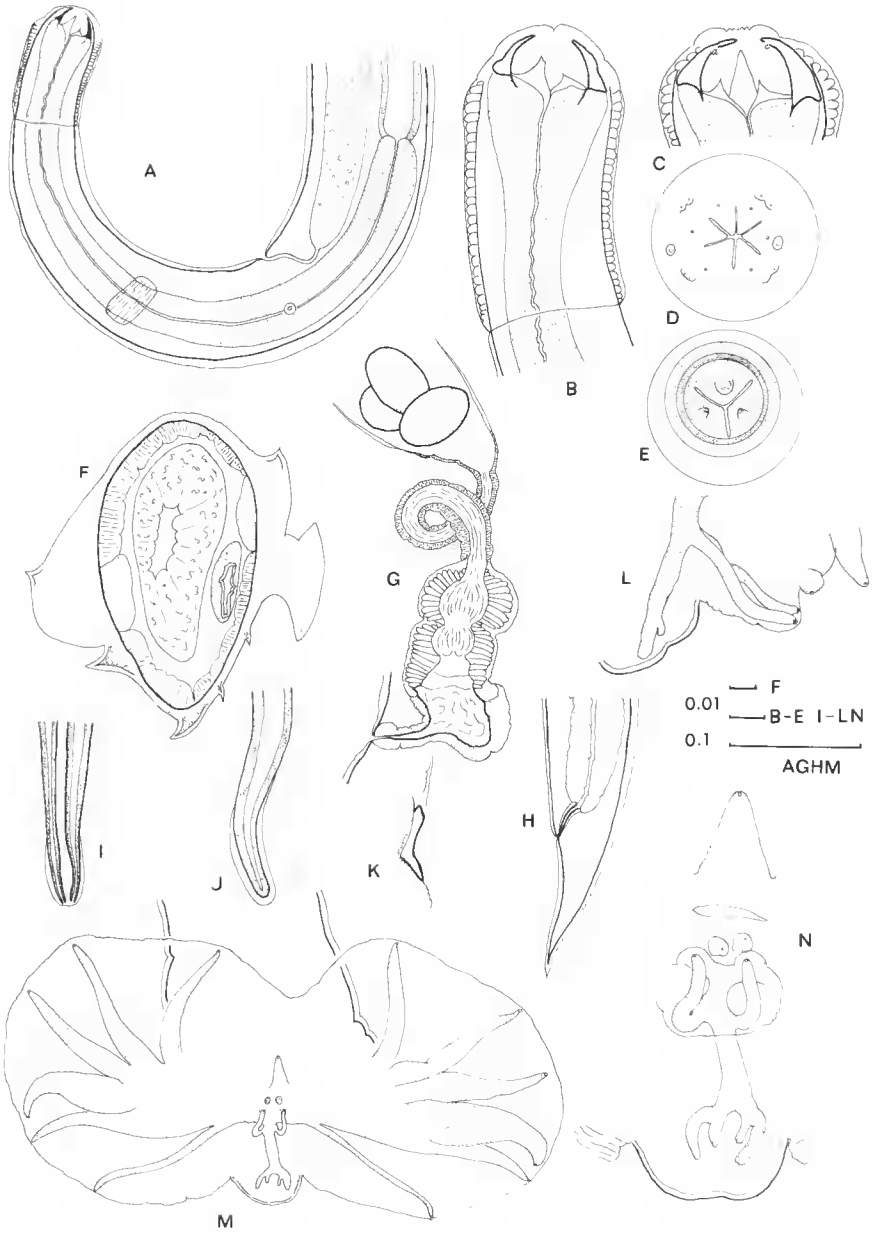

FIG. 6. — *Austrostrongylus incurvispiculum* sp. n. : A, anterior end, lateral view ; B, head, lateral view ; C, head, ventral view ; D, mouth, apical view ; E, optical transverse section through buccal capsule and teeth ; F, transverse section of mid-body region, ♂ ; G, ovejector, lateral view ; H, female tail, lateral view ; I, spicule tip, ventral view ; J, spicule tip, lateral view ; K, gubernaculum, lateral view ; L, dorsal lobe of bursa and genital cone, lateral view ; M, bursa, ventral view ; N, dorsal lobe of bursa and genital cone, ventral view. Scale lines in mm.

Head : Mouth opening with six small, sub-triangular lips, each with tiny internal papilla at base ; two amphids and four double submedian papillae present external to lips. Buccal capsule small, sub-globular, well sclerotised, circular in transverse section ; single dorsal tooth and two smaller sub-ventral teeth project into buccal capsule ; cephalic vesicle prominent ; oesophagus slender, claviform ; nerve ring in mid-oesophageal region ; excretory pore in posterior oesophageal region ; deirids at level of excretory pore.

Male : Length 4.0-5.1 (4.2) ; cephalic vesicle 0.070-0.085 (0.080) ; buccal capsule 0.020-0.027 (0.023) × 0.020-0.027 (0.024) ; dorsal tooth 0.010-0.015 (0.013) ; oesophagus 0.32-0.45 (0.40) ; nerve ring 0.27 from anterior end ; deirids 0.40 from anterior end ; spicules 0.58-0.77 (0.65) ; spicule tip blunt, slightly recurved ; spicules united at tip in very narrow cuticular expansion ; gubernaculum 0.025-0.040 (0.034). Bursa symmetrical ; dorsal lobe small, thickened ; rays 2 and 3 slender, terminate separately : rays 4 and 5 broad, ray 5 directed posteriorly at termination ; ray 6 narrower, almost straight ; ray 8 filiform, arising close to base of ray 9 ; ray 9 with recurved lateral branches, running ventrally and terminating in two prominent projections dorsal to papillae 7 ; main bifurcation of ray 9 near extremity, with two short internal and two external branches. Genital cone prominent non-sclerotised ; anterior lip conical ; posterior lip with two prominent rounded projections bearing papillae 7.

Female : Length 4.9-6.4 (5.4) ; cephalic vesicle 0.07-0.09 (0.08) ; buccal capsule 0.020-0.025 (0.022) × 0.023-0.036 (0.029) ; dorsal tooth 0.012-0.015 (0.014) ; oesophagus 0.40-0.52 (0.44) ; nerve ring not seen ; excretory pore 0.026-0.045 (0.035) from anterior end ; deirids 0.47 from anterior end ; tail 0.060-0.090 (0.076) long, simple, tapering ; vulva 0.37-0.46 (0.42) from posterior end ; *vagina vera* short, 0.04-0.05 (0.04) ; monodelphic ; posterior branch of reproductive tract absent : ovejector 0.08-0.11 (0.10) long ; eggs 0.07-0.09 (0.08) by 0.05-0.06 (0.05).

Discussion

Among species with two prominent lateral floats and four ventral body ridges, *A. incurvispiculum* is distinguished from *A. aggregatus* in having spicules shorter than 0.80 mm and from *A. victoriensis, A. thylogale* and *A. notoryctis* in having spicules longer than 0.40 mm. It differs from *A. paratypicus* and *A. macropodis* in lacking broad alae on the spicule tips, described in the latter species by Mawson (1973), and in the fact that the female of *A. incurvispiculum* is monodelphic. *A. incurvispiculum* is closest to *A. chandleri* in the characters of the dorsal ray, and in having the lateral branches pass ventrally to terminate in projections slightly dorsal and posterior to papillae 7. This feature was not described in *A. chandleri* by Mawson (1973) but was noted in comparing the new species with specimens of *A. chandleri* from *Macropus rufogriseus* from Emuvale, Queensland (MNHN 806 CA), a locality close to that where the host of the types of *A. chandleri* was collected. The spicules of *A. incurvispiculum* lack the inflated tip which was described by Mawson (1973) in *A. chandleri* and reconfirmed by us in examining new material. The two species also differ since the female of *A. incurvispiculum* is monodelphic. The only species of the

genus known to date with monodelphic females is *A. hypsiprymnodontis*, however, in this paper, *A. hypsiprymnodontis* is transferred to the genus *Paraustrostrongylus*.

No other species of *Austrostrongylus* are known to occur in *M. fuliginosus* in spite of extensive collecting of this host species (Beveridge and Arundel, 1979). At the site where these specimens were collected, *M. fuliginosus* occurs with *M. irma*, and may well have acquired the parasite from the latter host, since all the *Macropus* species closely related to it (*M. eugenii, M. rufogriseus, M. dorsalis*) are hosts of *Austrostrongylus* spp.

Paraustrostrongylus hypsiprymnodontis (Mawson, 1973) comb. nov.

Material examined : From *Hypsiprymnodon moschatus* Ramsay, 1876 ; Queensland : numerous specimens, Lammins Hill near Atherton, 18.VI.1982, coll. D. M. Spratt and R. Speare (AHC 12120 ; MNHN 541 HD).

Discussion

Humphery-Smith (1981) re-examined paratype material of this species and discussed its somewhat ambiguous taxonomic position. According to him, *Austrostrongylus hypsiprymnodontis* has monodelphic females, has ray 2 quite divergent from the remaining bursal rays and lacks ventral teeth, all of which are characters of *Paraustrostrongylus* Mawson, 1973, rather than *Austrostrongylus*. However, the principal character separating the two genera is a sclerotised genital cone which is present in *Paraustrostrongylus* but absent in *Austrostrongylus*. Neither Mawson (1973) nor Humphery-Smith (1981) could detect a sclerotised genital cone in *A. hypsiprymnodontis*. In the abundant new material available, a sclerotised genital cone is clearly present, and because *A. hypsiprymnodontis* therefore possesses all the characters of the genus *Paraustrostrongylus*, it has been transferred to the latter genus. The paratypes of *A. hypsiprymnodontis* (AHC 5449) were re-examined and conform exactly with the new material. Because the specimens are dark brown in colour, the sclerotisation of the genital cone is detectable only with difficulty.

CONCLUSIONS

The synlophe

Austrostrongylus and *Paraustrostrongylus* are unusual among Trichostrongyloidea in having lateral cuticular inflations or floats running down either side of the body, although a cuticular inflation resembling a float also occurs in one species of *Patricialina* Inglis, 1968, namely *P. birdi* Humphery-Smith and Durette-Desset, 1981. While this is clearly an evolved character, there has been no indication to date as to how these structures have evolved.

The present suite of new species of *Austrostrongylus* and *Sutarostrongylus* provides a series in which the evolution of the floats can be traced.

In *S. kirkpatricki* (fig. 1 F, G, H) there is no indication whatever of the development of floats. A basic synlophe of four ventral ridges directed to the left with a single right and a single left dorsal ridge conforms to the basic pattern present in all *Austrostrongylus* species.

A. safestatus has three ventral body ridges and three dorsal ridges in the anterior part of the body (fig. 2 F-L), with a reduction in the number of ridges posteriorly. However, a small float is present on the left hand side of the body. It is very small in the female and in the anterior part of the male body, but towards the posterior end of the male, it forms a distinct float. At this same level in the male, there is a very slight thickening on the right side of the body suggestive of a second poorly developed float. The related species, *A. petrogale* shows an increase in the number of body ridges to nine in the mid-body region. The ninth ridge is tiny and is only present for a short distance in the middle of the body. There is a marked reduction in the number of ridges posteriorly (fig. 3 L). A distinct float is present on the left side of the body but diminishes in size posteriorly in the female (fig. 3 K, L) while in the male, it attains its maximum size at the level of the anterior end of the spicules (fig. 3 F). The cuticle of the right dorsal field of both sexes is thickened and bears two prominent crests, but there is no indication of the development of a float. All the remaining species of *Austrostrongylus* have well developed right and left floats which generally extend from the cephalic vesicle to the bursa in the male and usually to the vulva or beyond in the female. The basic pattern of four, or less frequently three, ventral ridges gives the synlophe a frontal orientation. The right float always bears two ridges, one directed ventrally, the other dorsally, and a third, dorsal ridge is usually present, but sometimes only in the mid-body region (*A. bancrofti, A. minutus*). The left float possesses one or sometimes two ridges. Rarely (*A. notoryctis*) a distinct ridge is not present, but a single thickening of the cuticle exists, suggesting a ridge. Thus, in all the species of *Austrostrongylus* parasitic in *Macropus* and *Wallabia*, the synlophe is relatively uniform and conforms to the pattern already described (Mawson, 1973 ; Durette-Desset, 1979). This complex synlophe has evolved from species with the same pattern of body ridges, but without lateral body floats, now placed in a new genus *Sutarostrongylus*.

Relationships of *Austrostrongylus* and *Sutarostrongylus*

The addition of new species of *Austrostrongylus* necessitates a redefinition of the genus, allowing for the presence of a single body float and as few as six body ridges. *Sutarostrongylus* lacks floats but possesses six ridges. In both genera, the orientation of the synlophe is frontal, and in this respect they differ from *Dessetostrongylus* and *Beveridgiella* which have an oblique axis of orientation (Humphery-Smith, 1983). Species of *Dessetostrongylus* are monodelphic, while species of *Beveridgiella* have more than two dorsal ridges, further differentiating the genera from *Austrostrongylus* and *Sutarostrongylus*. *Patricialina* has a frontally oriented synlophe, but has four or five dorsal body ridges.

All species of *Austrostrongylus* and *Sutarostrongylus*, irrespective of their synlophe have a markedly inflated dorsal lobe of the bursa which does not occur in the other genera.

Paraustrostrongylus differs from *Austrostrongylus* in having a complex, sclerotised genital cone, in lacking ventral teeth or having reduced ventral teeth, and in having ray 2 of the bursa markedly divergent from and almost perpendicular to the remaining rays. Females of *Paraustrostrongylus* are monodelphic while all species of *Austrostrongylus* except *A. incurvispiculum* are didelphic.

Relationships of species within the genus

Using the principle morphological characters of the synlophe, the spicules and the bursa, the relationships of the various species can be established at least between groups of species.

1 — *Floats* : The features of the synlophe of *Austrostrongylus* have been discussed above. Because body floats are present only in *Austrostrongylus* and *Paraustrostrongylus* and in virtually no other trichostrongyloid genera, they are considered an evolved character. Consequently, *Sutarostrongylus* and *S.* sp., lacking floats, are considered primitive. *A. petrogale* and *A. safestatus* each with a single float are considered intermediate, and the remainder of the genus with paired floats, evolved.

2 — *Synlophe* : In many trichostrongyloid genera (Durette-Desset, 1971), an augmentation of the number of body ridges occurs with evolution. Applying this principle *S. kirkpatricki* and *Sutarostrongylus* sp. must be considered with six ridges. *A. safestatus* comes next with seven and the remainder of the genus with eight or nine are considered the most highly evolved.

3 — *Bursa* : In the Trichostrongyloidea, bursal asymmetry is an apomorphic character, since the primitive trichostrongyloid genera as well as other bursate nematode groups have symmetrical bursae. *Sutarostrongylus* and species of *Austrostrongylus* considered to have a plesiomorphic synlophe have also a symmetrical bursa. In the species with apomorphic synlophe characters, various degrees of bursal asymmetry occur. In *A. minutus, A. incurvispiculum, A. chandleri, A. wallabiae* and *A. aggregatus*, the bursa is symmetrical, or almost symmetrical. In *A. victoriensis, A. paratypicus, A. thylogale, A. bancrofti* and *A. macropodis* [the latter according to the drawing of Chandler (1924)], there is an asymmetry in the bursa, with the right lobe larger than the left and some dissimilarity in the size of the rays. *A. notoryctis* has a grossly asymmetrical bursa with an enlarged right lobe and virtually all the rays of dissimilar size.

4 — *Spicules* : Within the trichostrongyloid nematodes, short spicules are generally thought to be plesiomorphic in character (Durette-Desset, 1971). Thus within *Austrostrongylus*, there is a general correlation between spicule length and characters of the synlophe. All species which are classed as plesiomorphic according to synlophe characteristics also have short spicules (< 0.30 mm long). Furthermore, species of *Sutarostrongylus*, without floats and with few ridges, are characterised by striated spicules, similar to those occurring in *Dessetostrongylus*. The genus *Austrostrongylus* can therefore be divided into species with the plesiomorphic character of short spicules less than 0.30 mm long, and species with the apomorphic state, spicules longer than 0.30 mm.

5 — *Additional characters* such as the morphology of the spicule tips and the presence of a spine on the female tail are of use only at the specific level. The termination of the lateral branches of ray 9 posterior to the genital cone is considered apomorphic and clearly associates *A. chandleri* with *A. incurvispiculum*. Monodelphy occurs only in *A. incurvispiculum* but using the Trichostrongyloidea generally as an out-group, it is considered an apomorphic character. The elongate *vagina vera* of *A. aggregatus* is also apomorphic when compared with related genera of the Herpetostrongylinae. Using the characters discussed above to establish relationships within the genus, the cladogram shown in figure 7 is obtained. It was not possible to decide otherwise than on arbitrary grounds whether to rank spicule length before or after bursal asymmetry. Because of this, the two characters were given equal rank and the species divided into three equivalent groups using the two characters.

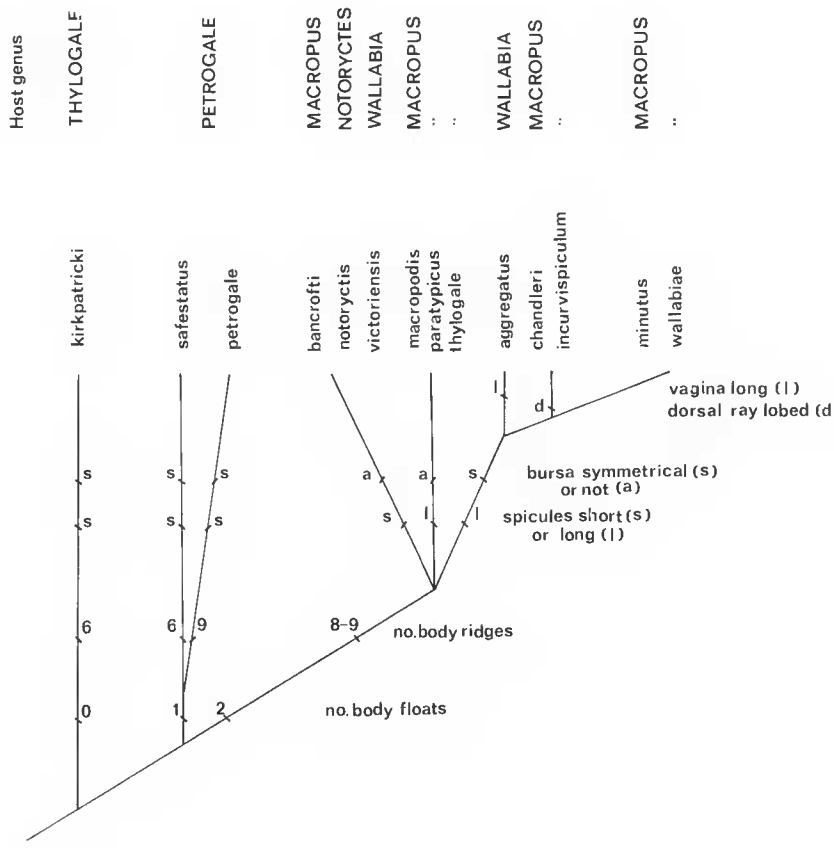

FIG. 7. — Cladogram showing possible genealogical relationships of species of *Austrostrongylus*.

Correlation with hosts

The origins of *Austrostrongylus* and *Sutarostrongylus* appear to lie with some *Woolleya* Mawson 1973, some parasitic in small dasyurid marsupials (fig. 8). The species of *Sutarostrongylus*, with generally plesiomorphic characters, occur in *Thylogale stigmatica* and *T. thetis*. Two slightly more evolved species, *A. safestatus* and *A. petrogale*, occur in *Petrogale* spp. while the remaining species of the genus, *Austrostrongylus*, all possessing paired floats, occur in the genus *Macropus* and principally in the subgenus *Prionotemnus* (exceptions are discussed below).

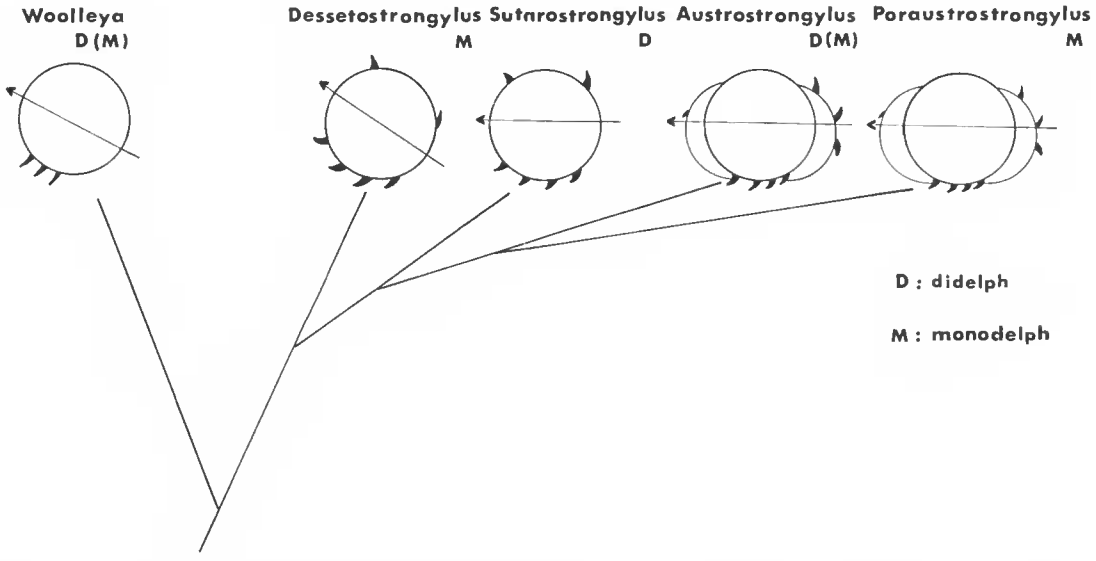

Fig. 8. — Relationships of *Austrostrongylus* and *Sutarostrongylus* with related genera of the Herpetostrongylinae.

Therefore, the *Austrostrongylus* lineage appears first to have invaded *Thylogale* spp., evolved further in *Petrogale* spp. and undergone a major radiation centred on *Prionotemnus* spp. *(Macropus eugenii, M. dorsalis, M. rufogriseus)*. The evolution of the parasites is parallel to that of the hosts, since the *Thylogale-Petrogale* group of genera is considered more ancient than the modern *Macropus* spp. both on traditional morphological grounds (Sanson, 1978) and from electrophoretic data (Richardson and McDermid, 1978). Species of *Macropus (Prionotemnus)* in which most of the evolved species of *Austrostrongylus* occur are small scrub wallabies, and this subgenus may be ancestral to the other subgenera of *Macropus* (Sanson, 1978). Of the eleven species of *Austrostrongylus* sharing apomorphic character states, seven occur in species of *Prionotemnus*. *A. thylogale*, described originally from *Macropus eugenii*, also occurs in *Setonix brachyurus* (Quoy and Gaimard, 1830) on Rottnest Island, Western Australia (Thomas, 1959 ; Inglis, 1968) but this can be

explained as a capture, since *A. thylogale* also occurs in *M. eugenii* in the same general geographic region. Similarly, *A. incurvispiculum* is probably a parasite of *M. irma* (also a species of *Prionotemnus*) since *M. fuliginosus* is not normally a host for *Austrostrongylus* spp. (BEVERIDGE and ARUNDEL, 1979) but where it is infected with *A. incurvispiculum, M. fuliginosus* is sympatric with *M. irma*. Two species, *A. aggregatus* and *A. victoriensis*, occur exclusively in *Wallabia bicolor*. The relationships of *Wallabia* with *Prionotemnus* are not clear, but *Wallabia* may belong to an older lineage from which *Prionotemnus* was derived (SANSON, 1978). *W. bicolor* however inhabits similar habitat and is frequently sympatric with *M. dorsalis* and *M. rufogriseus*. Therefore species *A. victoriensis* and *A. aggregatus* may represent transfers from *Macropus* to *Wallabia*. *A. chandleri* occurs in both *W. bicolor* and *M. rufogriseus* (MAWSON, 1973).

A. aggregatus has a singularly long vagina which is apomorphic with respect to *Dessetostrongylus* or *Woolleya*, suggesting that *A. aggregatus* may have been derived from the related species *A. wallabiae* or *A. minutus* and may therefore be a transfer from a *Prionotemnus* species to *Wallabia*. However, *A. victoriensis* cannot be accounted for in a similar way as it is plesiomorphic in spicule characters and may be related to the ancestors of species of *Austrostrongylus* in *Macropus* spp., with *A. bancrofti* in *M. dorsalis* being derived from a similar ancestor.

A. notoryctis parasitises the mole, *Notoryctes typhlops*, a host unrelated to the Macropodidae. Morphologically *A. notoryctis* is aberrant and was presumably captured from macropodids, its common ancestry being with *A. minutus* and *A. victoriensis* in *M. dorsalis* and *W. bicolor* respectively.

In spite of the exceptions noted, the macropodine subgenus *Prionotemnus* has been a centre of radiation for *Austrostrongylus* spp., though exclusively in the south of the continent. No *Austrostrongylus* species are known from *M. agilis* (SPEARE *et al.*, 1983) and *M. parryi* (BEVERIDGE, unpublished observations), both northern species of *Prionotemnus*, and the status of *M. parma* is unknown since very few collections of parasites have been made from it. Both *M. dorsalis* and *W. bicolor* are parasitised by *Austrostrongylus* in the southern part of their respective ranges, as far north as the Burnett River region of Central Queensland but neither species is infected in northern Queensland (BEVERIDGE, unpublished observations).

No reasons for the southern focus are obvious, and it is largely the plesiomorphic species of *Austrostrongylus* as well as *Sutarostrongylus* which occur in the north in *Thylogale* spp. and *Petrogale* spp.

With the transfer of *A. hypsiprymnodontis*, the genus *Paraustrostrongylus* now consists of species inhabiting the Potoroinae (Macropodidae), Phalangeridae, Petauridae with one species in a rodent. All of these marsupial groups are phylogenetically older than the Macropodinae, but have been invaded recently, since *Paraustrostrongylus* is considered to have been derived from *Austrostrongylus* (HUMPHERY-SMITH, 1983). In this instance, the evolution of the parasites in no way follows that of the hosts, but appears to be almost at random, infecting terrestrial browsers (Potoroinae), arboreal folivores (*Trichosurus*) and arboreal nectar feeders (*Gymnobelideus*). Invasion of the rodent *Rattus fuscipes* (Waterhouse, 1839) is an extremely recent capture (OBENDORF, 1979) since the genus *Rattus* has only been present on the Australian continent for about one million years (WATTS and ASLIN, 1981).

Acknowledgements

Our thanks are due to S. Barker, R. Close, P. M. Johnson, T. H. Kirkpatrick, R. Speare, D. M. Spratt and P. M. Thomas for collections of specimens, and to D. M. Spratt and E. Walter for reading an early draft of the manuscript. Collecting by S. Barker and R. Close was assisted by a grant from the Australian Biological Resources Survey.

REFERENCES

Baverstock, P., M. Adams and I. Beveridge, 1985. — Biochemical differentiation in bile duct cestodes and their marsupial hosts. *Molec. Biol. Evol.* (in press).

Beveridge, I., and J. H. Arundel, 1979. — Helminth parasites of grey kangaroos *Macropus giganteus* Shaw and *M. fuliginosus* (Desmarest), in eastern Australia. *Aust. Wildl. Res.*, **6** : 69-77.

Beveridge, I., and M.-C. Durette-Desset, 1985. — Two new species of nematode (Trichostrongyloidea) from the marsupial mole *Notoryctes typhlops* (Stirling). *Bull. Mus. natn. Hist. nat., Paris*, 4e sér., **7**, sect. A, (2) : 341-347.

Cassone, J., 1983. — *Austrostrongylus victoriensis* n. sp. (Nematoda, Trichostrongyloidea) parasite de *Wallabia bicolor* (Marsupialia, Macropodidae). *Bull. Mus. natn. Hist. nat., Paris*, 4e sér., **5**, sect. A, (3) : 767-770.

Chandler, A. C., 1924. — A new genus of trichostrongylid worms from the kangaroo. *Parasitology*, **16** : 160-163.

Durette-Desset, M.-C., 1971. — Essai de classification des Nematodes Héligmosomes. Corrélations avec la paléobiogéographie des hôtes. *Mém. Mus. natn. Hist. nat., Paris*, n.s., sér. A, Zool., **49** : 126 p.

— 1979. — Compléments morphologiques à l'étude des genres *Austrostrongylus* Chandler, 1924, et *Paraustrostrongylus* Mawson, 1973 (Nematoda, Trichostrongyloidea). *Bull. Mus. natn. Hist. nat., Paris*, 4e sér., **1**, sect. A, (4) : 1023-1030.

— 1982. — Relations hôtes-parasites chez les Trichostrongyloides. *Mém. Mus. natn. Hist. nat., Paris*, n.s., sér. A, Zool., **123** : 93-101.

Humphery-Smith, I., 1980. — *Beveridgiella* n. gen., *Dessetostrongylus* n. gen. (Nematoda, Trichostrongyloidea) parasites de Marsupiaux australiens. *Bull. Mus. natn. Hist. nat., Paris*, 4e sér., 1980 (1981), **2**, sect. A, (4) : 999-1012.

— 1981. — *Paraustrostrongylus gymnobelideus* n. sp. (Nematoda, Trichostrongyloidea) parasite de *Gymnobelideus leadbeateri* (Marsupialia, Petauridae) de Victoria, Australie. *Bull. Mus. natn. Hist. nat., Paris*, 4e sér., **3**, sect. A, (2) : 509-513.

— 1983. — An hypothesis on the evolution of the Herpetostrongylinae (Trichostrongyloidea : Nematoda) in Australian Marsupials, and their relationships with Viannaiidae, parasites of South American marsupials. *Aust. J. Zool.*, **31** : 931-942.

Inglis, W. G., 1968. — The geographical and evolutionary relationships of Australian Trichostrongyloid parasites and their hosts. *J. Linn. Soc.* (Zool.), **47** : 327-347.

Johnston, T. H., and P. M. Mawson, 1938. — Some nematodes from Australian marsupials. *Rec. S. Aust. Mus.*, **6** : 187-198.

Johnston, T. H., and P. M. Mawson, 1940. — Nematodes from South Australian Marsupials. *Trans. R. Soc. S. Aust.*, **64** (1) : 95-100.

MAWSON, P. M., 1973. — Amidostomatinae (Nematoda : Trichostrongyloidea) from Australian marsupials and monotremes. *Trans. R. Soc. S. Aust.*, **97** : 257-279.

MAYNES, G. M., and G. B. SHARMAN, 1983*a*. — Godman's rock wallaby *Petrogale godmani*. *In* : The Australian Museum Complete Book of Australian Mammals. Ed. R. STRACHAN. ANGUS and ROBERTSON, London : 215.

MAYNES, G. M., and G. B. SHARMAN, 1983*b*. — Proserpine rock wallaby *Petrogale persephone*. *In* : The Australian Museum Complete Book of Australian Mammals. Ed. R. STRACHAN. ANGUS and ROBERTSON, London : 220.

OBENDORF, D., 1979. — The helminth parasites of *Rattus fuscipes* (Waterhouse) from Victoria, including description of two new nematode species. *Aust. J. Zool.*, **27** : 867-879.

RICHARDSON, B. J., and E. M. MCDERMID, 1978. — A comparison of genetic relationships within the Macropodidae as determined from allozyme, cytological and immunological data. *Aust. Mammal.*, **2** : 43-52.

SANSON, G. D., 1978. — The evolution and significance of mastication in the Macropodidae. *Aust. Mammal.*, **2** : 23-28.

SHARMAN, G. B., and G. M. MAYNES, 1983. — Unadorned rock wallaby *Petrogale inornata*. *In* : The Australian Museum Complete Book of Australian Mammals. Ed. R. STRACHAN. ANGUS and ROBERTSON, London : 213-214.

SPEARE, R., I. BEVERIDGE, P. M. JOHNSON, and L. CORNER, 1983. — Parasites of the agile wallaby, *Macropus agilis* (Marsupialia). *Aust. Wild. Res.*, **10** : 89-96.

THOMAS P. M., 1959. — Some nematode parasites from Australian hosts. *Trans. R. Soc. S. Aust.*, **82** : 151-162.

WATTS, C. H. S., and H. J. ASLIN, 1981. — The Rodents of Australia. ANGUS and ROBERTSON, London.